Do Male House Wrens (*Troglodytes aedon*) Vary Their Singing Among Various Reproductive Stages?

Research Thesis

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Abstract

The vocalizations of male songbirds can function in attracting mates and in defending territory. If song were used for attracting a mate, song output should decline following pairing. If song were used primarily for territory defense, song output should be constant throughout reproduction, because territories are maintained throughout multiple reproductive attempts within one breeding season. If song were used for communicating an 'all clear' signal, song output would be highest during incubation, when females are spending the most time on the nest. The purpose of this study was to determine whether the song of male House Wrens (*Troglodytes aedon*) changes throughout the reproductive cycle. Male House Wren song was recorded by attaching a microphone to the nesting box during four different stages of reproduction (nest-building, laying, incubation, and nestling feeding). The vocalizations were analyzed for song rate (# songs/minute), duration (length of each song), and frequency. Song rate was greatest during the pre-laying stage. Song length was lowest during nestling stage. Results indicate that song may be used primarily for finding mates, and not territory defense or as an 'all clear' signal. However, I may not be detecting song used during territorial defense, as our microphone was stationary and located on the nesting box. Future studies should follow individual males to determine whether males also sing away from the nest box, or shift the location of singing during the breeding season.

Introduction

Male songbird vocalization can function to attract mates, defend territory, or communicate with their mate. Song features that influence female choice when attracting

mates vary, but song output, song complexity, local song structure and vocal performance are considered important when attracting mates (Nowicki and Searcy 2004). Song is used for male-male interactions as well. When songbirds enter another's territory, the territory owners try to modify their territory response to best handle the threat and reduce the costs of territory defense (Briefer, Aubin, and Rybak 2009). Vocalizations can also function as an 'all clear' signal to females during nest-building, incubation, and raising young (Johnson and Kermott 1991). By using song as an 'all clear signal,' the female wren is able to leave or exit the nest without having to check for predators. Not having to check for danger saves the female wren valuable time and may allow for faster feeding and nest building.

Each songbird has a unique song in which frequency, amplitude, number of syllables, duration, and length can be analyzed. These song characteristics vary among individuals and are used during both female choice and male-male competition. In Zebra Finches, a high amplitude song was preferred by female wrens when choosing a mate (Ritschard, Riebel, and Brumm 2010). By increasing vocal amplitude, songbirds extend the active space of their songs which helps to broadcast their songs more effectively when interacting with a rival male (Brumm 2004).

House Wrens (*Troglodytes aedon*) are one type of songbird that utilizes vocalization for many different functions among the different stages of reproduction. One function of House Wren song in males is to attract a mate. When male House Wrens are trying to attract a mate, spontaneous songs are produced loudly in long bouts around unoccupied nest sites (Johnson 1998). Pre-nesting songs have been shown to attract females even when played from a speaker box, which provides strong experimental

evidence that song can function in attracting females for breeding (Johnson and Searcy 1996). The female wren usually settles with the first available male wren that is singing and has at least one high quality nest site (Eckerle and Thompson 2006). When House Wren populations become dense and there is strong sexual selection due to their polygamous mating system, there may be selective pressure for larger song repertoires and more complex singing behaviors (Kroodsma 1977). This refinement of song helps the male wren become more distinct, which may give the male a better chance of mating.

House Wren song may also be used to ward off other males who threaten part of their territory. Males do not direct song at neighbors or intruders on a routine basis, but do direct songs at other males especially in response to a newly settled neighbor (Johnson and Kermott 1991). The vocalizations would help communicate to other wrens their ownership of a territory. Wrens have been found to increase singing performance when observing a moving intruder compared to a stationary one (Amrhein and Lerch 2010). This could be interpreted as an increased effort in territory defense in the face of a greater territorial threat.

Considering that song is used during different stages of reproduction for various functions (attracting mates, communication of an ’all clear‘ signal, and territory defense), it is expected that the songs would change in frequency and duration according to the stage of reproduction. The goal of this study is to determine the function of song in House Wrens. If song is used for attracting a mate, song output and length should decline following pairing. If song is used primarily for territory defense, song output and length should be constant throughout reproduction, because territories are maintained throughout multiple reproductive attempts within one breeding season. If song is used

for communicating an ’all clear‘ signal to the female wren, I predict that song output would be highest during incubation, when females are spending the most time in the nest box.

Methods:

Study Species:

House Wrens were selected to study because they have short reproduction cycles and readily build nests in artificial nest boxes. The wrens are also polygamous and can have several nests in one breeding season. House Wren populations range from south Canada to areas of south Argentina and Chile and along several islands around Mexico. House Wrens migrate from the northern United States and southern Canada down to areas in southern United States, Mexico, Argentina and Chile (Johnson 1998). The wrens are characterized as a smaller songbird, 11-13 cm long, and are colored in different shades of brown and grey. Female wrens lay one egg per day to make an average clutch size around 6 eggs (Johnson 1998). Both male and female wrens help build the nest and feed young, but only the female is responsible for incubation.

House Wren song patterns and frequency of song differ among males. Most songs consist of “a series of very rapid notes, the pitch rising at the beginning, falling towards the end, with a sudden increase in loudness on the highest notes in the middle of the song” (quoted in Johnson 1998). The number of syllables per song ranges from 3 to 22, with a mean of 11.49 (Platt and Ficken 1987). Recordings ranged from 0.33 to 2.48 seconds in length with a mean of 1.25 seconds and syllables ranged in frequency from 1.5 to 8.0 KHz.

Study Site:

Research was conducted near Lima, Ohio USA, between the months of May and August 2012. A total of 117 House Wren nesting boxes were established in three habitats: 40 boxes in wooded area next to campus (40.7363927° N, 84.0266254°W), 37 boxes in a local residential/industrial area (40.747556° N, 84.034588°W), and 40 boxes on the Hawthorn Hills Golf Course (40.752005°N, 84.036931°W).

Nesting Observations:

All nesting boxes were checked twice a week. When egg laying or hatching was expected, the box was checked daily. Laying stage was expected when a cup with a lining was established in the bird box. Hatching was determined to take place after 12-13 days of incubation had passed (Bowers et al. 2012).

Song Recording and Analysis:

Thirty minutes of House Wren song were recorded during four different stages of reproduction: pre-laying, laying, incubation, and nestling feeding. Pre-laying was distinguished by having around 4 centimeters of nest material or a cup having been formed. The laying stage consisted of 4 eggs or fewer having been laid. Incubation was the period in which 5-7 days had passed since the last egg was laid. The nestling stage was 4 days after ≥50% of the eggs had hatched.

Recordings were made with a Marantz PMD-660 digital recorder and an Audio Technica shotgun microphone. Recordings were taken between the hours of 0600 and 1200. The microphone was tied with a bungee cord to the metal pole that supported the nesting box and pointed up toward the box. Researchers moved at least 60 m from the

box during the recording to ensure no researcher interference. The date, box number, nest contents, and start time were recorded.

Program Signal (Version 4.04.29, Cambridge Electronic Devices 2008, Cambridge, UK) was used to measure song rate, song length, mean frequency, and maximum frequency for a selected fifteen minute period of each song recording. Each fifteen minute period was chosen from the point at which the focal male first began singing. Song length, mean frequency, and maximum frequency were measured only for songs that were clearly recorded (little background noise) using a customized program within Program Signal developed by D. Nelson (unpub. data). If a song occurred, but there was interference from background noise, the song was noted for the total number of songs in 15 min, but length and frequency were not measured. Song rate, song length, mean frequency, and maximum frequency were averaged for each time period.

Program JMP (Version 9.0.0, SAS Institute Inc. 2010, Cary, NC) was used to compare reproductive stage (pre-laying, laying, incubation, and nestling feeding) with song rate, song length, mean frequency, and maximum frequency. Sample sizes vary because it was not possible to obtain song recordings from every male and some nests were depredated.

Results

Of the 117 boxes that were available to the wrens, only 44 boxes were used as nesting sites at least once throughout the season. A total of 113 recordings of House Wrens at these 44 nest boxes were obtained between the months of May and August 2012. Within the 113 recordings, 4263 individual male songs were analyzed.

Song length and rate declined with nesting stage, being rapid and long during the pre-laying stage and slow and short during the nestling feeding stage. Song rate did not vary among laying, nestling and feeding stages, but was greater during the pre-laying stage compared to the other stages ($P = 0.003$, Figure 1), and did not change with date ($P = 0.11$; overall, $F_{4,108} = 3.68$, $P = 0.008$). Song length did not vary among incubation, laying, and pre-laying stages, but was shorter during the feeding stage compared to the other stages ($P = 0.0005$, Figure 2), and declined with date ($P = 0.02$, Figure 3; overall, $F_{4,110} = 8.93$, $P < 0.0001$).

Discussion

Because songs during pre-laying were rapid and long, and songs during nestling feeding were slow and short, I conclude that House Wrens use song mostly for mate attraction. Because I saw changes in song with respect to reproductive stage, not a consistent song rate and length throughout breeding, patterns of House Wren song do not support the predictions of the territoriality hypothesis. The hypothesis that House Wrens song functioned mostly as an ’all clear‘ signal was not supported, as song output was low during incubation.

The highest level of song rate was found in the pre-laying stage of reproduction, suggesting song is important in initial mate pairing. Johnson and Kermott (1991) found similar results when the pre-laying stage had the highest amount of spontaneous song, which was followed by a sharp decline in song following pairing. Males who find mates quickly increase their chance of breeding successfully and may have opportunities to produce a second clutch. Males would therefore have a high song rate before pairing despite the energetic cost of singing. In Carolina Wrens (*Thryothorus ludovicianus*), the

energetic cost of singing was found to be three to nine times the basal metabolic rate (Eberhardt 1994). Future research should examine whether song output after the first female has initiated incubation affects likelihood for polygynous mating.

Song length was found to decrease in the nestling stage of reproduction. This finding is similar to the reports from previous years at this location. In 2011, the nestling stage song length was considerably lower compared to the laying and incubation stages (Schafer 2012). Because both parents help care for the nestlings by feeding and removing feces for 10-15 days after fledging (Morrison and Johnson 2012), song length may be lower to account for the energetic demands of nestling feeding. Energy used to make longer songs may be decreased to make up for the energy lost for feeding. Song would be used for simple communication like for the ’all clear‘ signal and territory defense (Johnson and Kermott 1991), which would not use much energy and improve feeding time. Further research on energy usage during the nestling stage should be conducted to better understand if the amount of energy expenditure while taking care of young would result in less energy for song, which could lead to shorter song length.

Song length was found to decrease throughout the season after statistically controlling for breeding stage. One study found testosterone concentrations to be highest at the beginning of breeding season, which lead to corresponding increased length and song output (Riters et al. 2000). The testosterone levels then dropped after the breeding season, which led to a decline in song length and output. Testosterone levels in the wrens could possibly be one explanation for the decrease in song length. More research should be conducted on wrens to see if testosterone is directly related to song output and length as the season progresses.

Other studies of House Wrens did find evidence for the use of song for defending territory and as an 'all clear' signal. While collecting song to analyze syllables of House Wrens, Platt and Ficken (1987) found that the wrens tended to sing more rapidly when females were near or in the nest. Platt and Ficken's observation supports song as an 'all clear' signal as the wrens would be communicating to each other around the box. Johnson and Kermitt (1991) observed that male song was used for territory defense. When another male wren invaded a male wren's territory, song was directed at the intruder. Although I did not find evidence that House Wrens use song for territory defense or as an 'all clear' signal, additional research should be conducted which explicitly describes the context in which the song occurs. An observer could label certain songs as mate attraction, an 'all-clear' signal, or territory defense. The relative frequency of occurrence of each song type could be compared. This could help explain what functions of song are most important during each reproductive stage.

In summary, House Wren song does vary in length and rate throughout the breeding stages. This observational study suggests that song is important for attracting mates as the pre-laying stage produced the greatest song output. Song, therefore, should be just as important for male courtship displays in other songbirds. The decrease in song length for the feeding stage would suggest that songbirds would possibly spend more energy trying to care for young than singing or trying to attract multiple mates.

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FIGURE 1: The relationship between breeding stage and song rate of male House Wrens in Allen County, OH, May-August 2012. Different letters represent significant differences ($P < 0.05$) using a student's *t* test.

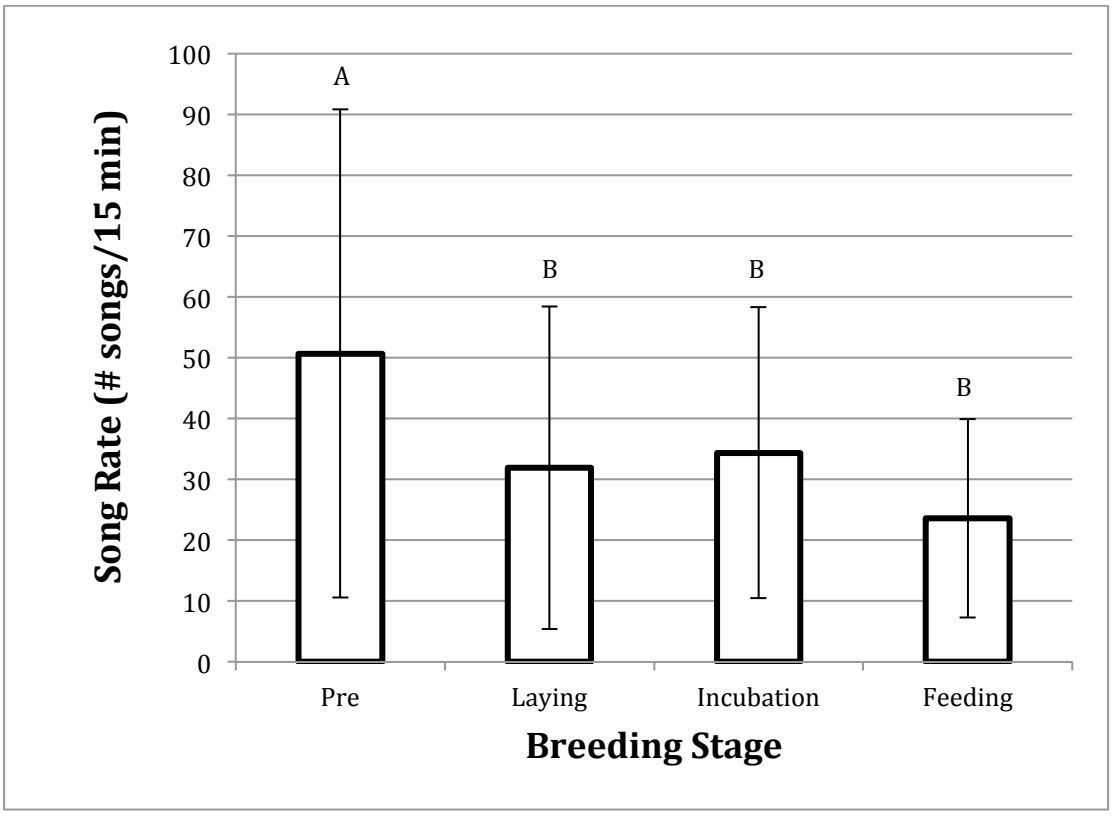

Figure 2: The relationship between breeding stage and song length of male House Wrens in Allen County, OH, May-August 2012. Different letters represent significant differences ($P < 0.05$) using a student's *t* test.

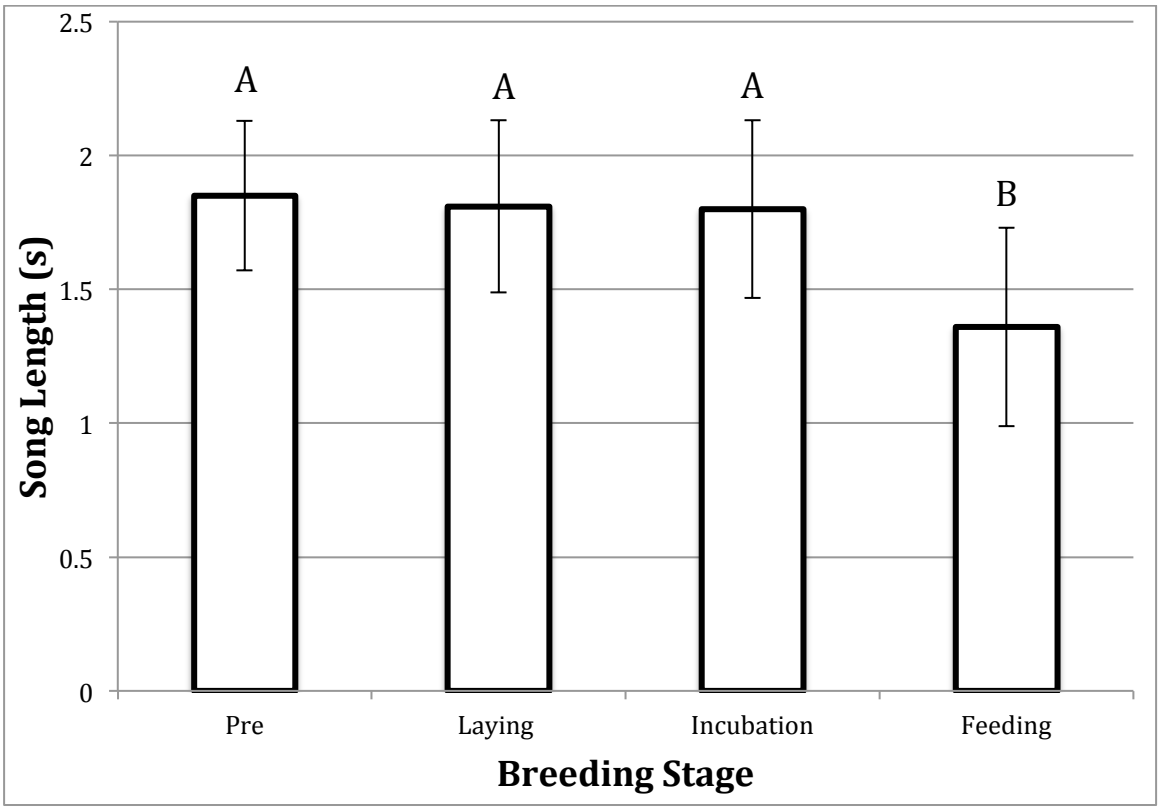

Figure 3: The relationship between date and song length of male House Wrens in Allen County, OH, May-August 2012.